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HABITAT ASSOCIATIONS OF MEXICAN SPOTTED OWL NEST AND ROOST SITES IN CENTRAL ARIZONA

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ABSTRACT.—We analyzed landscape characteristics surrounding Mexican Spotted Owl (*Strix occidentalis lucida*) nest and roost trees in Arizona at three spatial scales: one circular plot of 201 ha (800-m radius) and two 400-m-wide "ring" plots between 800 m and 1,600 m from each nest or roost tree. The percentages of vegetation types were significantly different between 51 owl and 51 random areas only within the 201-ha circular plots. Owls selected both mature and young mixed conifer forests that had high canopy closure (≥55%) more than expected based on availability. Owls selected pine (*Pinus* spp.) and pine-oak (*Quercus* spp.) forests in proportion to availability. Forty-one percent of all nests and roosts were located in mixed conifer forests, even though this forest type covered only 5% of the study area. Pine and pine-oak forests covered 78% of the study area, and 59% of nests and roosts were located in these forest types. The only forest type in which we did not locate nests and roosts was mature open canopy ponderosa pine (*P. ponderosa*) forest. Owls occupied areas of predominantly younger forests, but only if residual large (≥45.7 cm dbh) trees were present. Indices of landscape structure did not differ significantly between owl and random areas. Future management of Mexican Spotted Owls in areas of moderate topographic relief should focus on retention of mature forests, especially mixed conifer stands with canopy closure ≥55%. Residual large trees, especially Gambel oaks (*Q. gambelii*), are important microhabitat components in younger forests. *Received 19 February 2002, accepted 4 November 2002.*

The association between Spotted Owls (*Strix occidentalis*) and late seral stage forests has been documented for both the Northern (*S. o. caurina*) and California (*S. o. occidentalis*) subspecies (Gutiérrez et al. 1995). The habitat associations of the Mexican Spotted Owl (*S. o. lucida*) led in part to the listing of the subspecies (U.S. Dept. of Interior 1993, 1995), even though these associations were not understood as clearly as for the threatened Northern Spotted Owl (U.S. Dept. of Interior 1990). Limited evidence has suggested that Mexican Spotted Owls may not depend upon old growth forests to the same degree as the Northern and California Spotted Owls (Ganey and Balda 1989a, Seamans and Gutiérrez 1995).

Past research into the habitat requirements of Mexican Spotted Owls has included analysis of fine scale (≥0.2 ha) habitat selection (see review by Ganey and Dick 1995) and landscape scale (≥201 ha) habitat selection (Ganey and Balda 1994, Grubb et al. 1997, Ganey et al. 1999, Peery et al. 1999). These studies found that owls occupy mature forests with dense canopy cover. However, most of these previous studies were conducted in areas of mixed conifer forest and steep terrain. The Mexican Spotted Owl occupies a variety of environments in the Southwest, including mixed conifer forest, pine (*Pinus* spp.)-oak (*Quercus* spp.) forest, and canyons (Ward et al. 1995). We studied a Mexican Spotted Owl population occupying an area of moderate topography dominated by pine-oak forest. Therefore, our study broadens the understanding of habitat selection by Spotted Owls in the southwestern United States.

Data on the spatial configuration (e.g., fragmentation) of vegetation types around Mexican Spotted Owl nest and roost sites have been limited (Ganey and Dick 1995). Peery et al. (1999) found no difference in the spatial configuration of vegetation types between Mexican Spotted Owl sites and random sites in an area of steep terrain and mixed conifer forest in New Mexico. For the two coastal subspecies, some studies have reported Spotted Owls in areas less fragmented than the surrounding landscape (Hunter et al. 1995, Moen and Gutiérrez 1997) while other studies have found no difference between owl and random sites (Carey et al. 1992, Ripple et al. 1997). Therefore, we examined the spatial configuration of vegetation types around Mexican Spotted Owl nest and roost areas to estimate the utility of landscape metrics for dis-

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tinguishing Spotted Owl habitat on our study area.

The objective of our research was to estimate landscape scale habitat selection by Mexican Spotted Owls in northcentral Arizona. In particular, we predicted (1) landscapes around Spotted Owl nest and roost sites would contain more mature, closed canopy forest than landscapes around random sites, and (2) the spatial pattern of vegetation types in landscapes around Spotted Owl nest and roost sites would be less fragmented than the pattern of vegetation types in landscapes around random sites.

METHODS

Study area.—Our study area encompassed 585 km^2 of the Coconino National Forest (34° 51′ N, 111° 28′ W) and was located 40 km southeast of Flagstaff, Arizona. Primary land uses were timber harvesting, livestock grazing, and recreation. Selection harvest was the dominant timber management technique. The topography was gentle with several small cinder cones throughout the area; elevations ranged from 1,800 to 2,660 m.

Three major forest communities occurred within the study area. Mixed conifer forest was dominated by Douglas-fir (*Psuedotsuga menziesii*) and white fir (*Abies concolor*) with subdominant ponderosa pine (*Pinus ponderosa*), quaking aspen (*Populus tremuloides*), and Gambel oak (*Quercus gambelii*). Mixed conifer forest was present at higher elevations and on north-facing slopes. Pine-oak forest was dominated by ponderosa pine and Gambel oak, and was present at mid-elevations and on south-facing slopes. Lower elevations consisted of piñon-juniper woodland dominated by piñon pine (*Pinus edulis*) and junipers (*Juniperus deppeana* and *J. monosperma*).

The climate within the study area was characterized by cold winters (mean maximum daily temperature = 6° C) and warm summers (mean maximum daily temperature = 25° C). Precipitation occurred primarily from December through March in the form of snow; however, monsoon thundershowers were common from mid-July through September.

Owl and random locations.—We used standard Spotted Owl surveying techniques (Forsman 1983, Franklin et al. 1996) to locate nest and roost trees from April to August (i.e., breeding season) of each year. We attempted to capture all owls detected on the study area. We marked each captured owl with a numbered, locking aluminum leg band and a colored leg band on opposite legs. We used the colored leg bands (see Forsman 1983, Franklin et al. 1996) to identify individual owls and to assign individuals to unique territories.

We randomly selected one nest or roost tree per territory from among all those found from 1991 through 1996. By selecting one tree per territory we maintained sampling independence and obtained a location for centering owl sample plots in each territory. We established *a priori* an order of selection to reflect a continuum of stronger to weaker association with the activity center of a given territory. Our order of selection was (1) nest tree, (2) pair roost, (3) male roost. Therefore, we used a nest tree if one was available; otherwise, we selected a roost tree. Hereafter, nest and roost plots will be referred to as owl areas.

Using IDRISI 4.1 (Eastman 1994), we located a random set of comparison areas by generating random Universal Transverse Mercator (UTM) coordinates within the study area. We excluded locations that fell in water or large grassland areas. To maintain sampling independence, each random point was ≥2,400 m from any other random point. This distance represented the mean nearest neighbor distance between owl territory centers (n = 42) during 1993, the year of highest density. Hereafter, these random locations will be referred to as random areas.

We used a Trimble GeoExplorer™ global positioning system to record the center of owl and random areas accurately. We conducted differential correction of all locations using base station data from either the Coconino National Forest Supervisor Office or USGS Colorado Plateau Research Station, both located in Flagstaff, Arizona.

Classification of vegetation types.—We used a Landsat 5 Thematic Mapper-based vegetation map developed by D. W. Farris (unpubl.). The initial Landsat image was taken on 14 June 1994 and included a buffer zone around the study area to allow analysis of owl and random areas whose centers fell close to the study area boundary. We conducted *a priori* vegetation sampling and iteratively verified map classification until image accuracy was ≥75% (May 2000).

We assessed the final accuracy of the map by first selecting a set of random UTM points. We then located each point in the field and assigned the surrounding area to a vegetation classification based on dominant species composition, dbh size classes, and canopy closure of trees (see Appendix). We used a wedge prism of 10 basal area factor to estimate trees in a variable radius plot (Dilworth 1981) centered at each UTM location. For each tree within the plot, we recorded species and dbh. We defined mature trees as those ≥45.7 cm dbh. We used a concave spherical densiometer to estimate canopy closure within each plot by calculating the mean of the measurements taken at each of the major compass directions at a distance of 10 m from the plot center. We defined areas ≥55% overhead cover as closed canopy. Finally, we compared the vegetation type assigned in the field to the predominant vegetation class within the 90- × 90-m corresponding area of the final Landsat map. We expressed accuracy as a percentage of agreement between field and image plots.

Analysis of vegetation types.—We used IDRISI 4.1 to delineate three concentric, nonoverlapping plots around each owl nest or roost tree and each random UTM location. The smallest plot was 201 ha (i.e., 800-m radius circle). The other two areas were 400-m-wide "ring" plots (see Swindle et al. 1999) measuring 1,200 m and 1,600 m to the outer edges. Previous studies found that areas of 201 ha may have an important influence on Spotted Owl habitat selection for nest and roost sites (Grubb et al. 1997, Meyer et al. 1998, and Swindle et al. 1999). The intermediate plot size corresponded to the mean nearest neighbor distance between owl territory centers on our study area during the year of highest density. The largest plot size represented the mean home range size of paired Mexican Spotted Owls (Ganey and Balda 1989b).

We measured characteristics of vegetation types using IDRISI 4.1 and FRAGSTATS 2.0 (McGarigal and Marks 1995). We used owl areas to estimate Spotted Owl habitat selection while random areas represented available habitat in the landscape. Between owl and random areas, we compared (1) the percentages of vegetation types within plots; and (2) the landscape pattern measured by mean patch size (ha), mean patch shape index, and contagion of patches (Li and Reynolds 1993). We set the minimum patch size equal to the image resolution (i.e., 30 × 30 m). We analyzed landscape pattern only within the 201-ha plots. We did not analyze landscape pattern within the ring plots because we felt the variables would be most meaningful when measured within a relatively uninterrupted landscape (i.e., one in which potential edge effects were minimized).

Li and Reynolds (1994) found that indices of landscape pattern were autocorrelated and quantified slightly different aspects of overall pattern (i.e., they were not independent). However, Riitters et al. (1995) found that two of the indices we chose, mean patch shape index and contagion, were independent based on principal component analysis of 85 maps representing various landscape patterns and physiographic regions. Therefore, we felt the indices we chose provided relatively independent assessments of landscape pattern between owl and random areas.

If owls are associated with extensive areas of a particular vegetation type, owl areas should have lower values for mean patch shape index while mean patch size and contagion should be greater. Because mean patch shape is a measure of the complexity of all patches in an area using a perimeter-to-area ratio, a lower value for owl areas suggests that owls are selecting habitat containing large core areas for nesting and roosting. Contagion is a measure of both distribution and degree of intermixing of vegetation types in a landscape and expresses the probability that two adjacent pixels (i.e., image cells) belong to the same vegetation type. Thus, a higher value of this metric for owl areas suggests that owls select landscapes containing clumps of similar habitat.

Data analysis.—The data used for these analyses were nonnormal and heteroscedastic. Therefore, we used the multiresponse permutation procedure (MRPP) of program BLOSSOM (Cade and Richards 2001) for all analyses. MRPP is a distribution free test analogous to ANOVA. MRPP uses permutations of the data from randomization theory to provide probabilities of type I error (Edgington 1987). We used a multivariate MRPP test to examine differences in all vegetation types collectively at each plot size. Where significant differences occurred, we used univariate MRPP tests to determine which vegetation type(s) were responsible for the differences. For landscape pattern comparisons, we used only univariate MRPP tests. Due to the nonnormality of the data, we present differences as medians with 25% and 75% quantiles. To avoid type I error, we adjusted the significance level for multiple comparisons using the formula ($P < 0.05/k$), where k was the number of variables tested.

Post hoc description of microhabitat characteristics in young forests.—Our analysis of landscape scale plots indicated that Mexican Spotted Owls selected areas containing young mixed conifer forest. Because this finding seemed contrary to previous Spotted Owl research, which has shown an association of owls with mature and old growth forests, we examined microhabitat characteristics around owl nest and roost trees in all types of young forest. We collected data within 0.04 ha surrounding owl nest and roost trees according to methods described by Seamans and Gutiérrez (1995). We summarized the occurrence of cavity nests and mature trees in these plots.

RESULTS

Classification of vegetation types.—We classified eight vegetation types (see Appendix) with a final map accuracy of 80% (n = 88 random plots) within the study area and 81% (n = 123 random plots) within the study area and its buffer zone combined. Errors were limited primarily to mature open canopy ponderosa pine forest being misclassified as young forests of ponderosa pine and ponderosa pine-Gambel oak. Because young forests of ponderosa pine and ponderosa pine-Gambel oak (see Appendix for vegetation type descriptions) represented owl habitat (i.e., contained nests and roosts) but mature open canopy ponderosa pine forest was not owl habitat, we did not combine these vegetation types further.

Owl and random locations.—From 1991 through 1996, we located 84 different nest trees and 193 different roost trees in 51 unique owl territories. We used 31 nests, 16 pair roosts, and 4 male roosts in our analysis. Density was 0.147 territorial owls/km^2 during 1993, the year of highest owl density. However, we found owl nests and roosts in only five of the eight vegetation types (Fig. 1). Therefore, the ecological density (density in the five vegetation types where we located

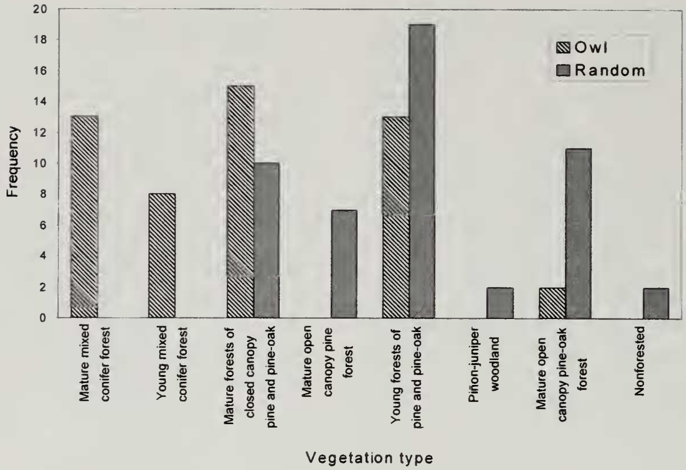

FIG. 1. Mexican Spotted Owls used mixed conifer forests for nesting and roosting more frequently than expected when compared to random locations on the Mexican Spotted Owl study area, central Arizona, 1991–1996. Owls used other vegetation types in proportion to availability.

nests or roosts; Tanner 1978) was 0.212 territorial owls/km^2 during 1993.

Analysis of vegetation types.—The percentages of vegetation types differed between owl areas and random areas only within 201 ha surrounding plot centers (multivariate MRPP, $P < 0.0001$). Univariate tests indicated that mature mixed conifer forest and young mixed conifer forest were responsible for differences, suggesting that owls selected landscapes containing these forest types. Canopy closure in both mixed conifer forest types was ≥55%. Owl areas contained a higher percentage of mature mixed conifer forest at the 201-ha scale than random areas (owl: median = 3.5%, 25% quantile = 0.6%, 75% quantile = 12.1%; random: median = 0.2%, 25% quantile = 0%, 75% quantile = 1.2%; univariate MRPP, $P = 0.0005$; Table 1). Owl areas contained a higher percentage of young mixed conifer forest at the 201-ha scale than random areas (owl: median = 1.5%, 25% quantile = 0%, 75% quantile = 10.3%; random: median = 0.2%, 25% quantile = 0%, 75% quantile = 1.3%; univariate MRPP, $P = 0.0002$; Table 1). The percentages of other vegetation types

TABLE 1. Landscapes within 201 ha (800-m radius circle) around 51 Mexican Spotted Owl nest and roost sites contained significantly higher median percentages of mature and young mixed conifer forests than landscapes around 51 random sites in central Arizona. Landscapes contained other vegetation types in proportion to availability.

	Owl			Random		
		Quantiles			Quantiles	
Vegetation type	Median	25%	75%	Median	25%	75%
Mature mixed conifer forest*	3.5	0.6	12.1	0.2	0.0	1.2
Young mixed conifer forest*	1.5	0.0	10.3	0.2	0.0	1.3
Mature closed canopy forests of ponderosa pine and ponderosa pine-Gambel oak	17.9	9.9	26.0	12.9	5.7	23.5
Mature open canopy ponderosa pine forest	4.9	2.3	11.5	11.5	6.1	18.7
Young forests of ponderosa pine and ponderosa pine-Gambel oak	41.5	31.6	50.7	39.5	32.0	51.5
Piñon pine-juniper woodland	0.0	0.0	0.2	0.1	0.0	1.2
Mature open canopy ponderosa pine-Gambel oak forest	7.5	3.7	10.3	10.4	4.9	17.5
Nonforested	5.5	2.5	9.8	11.3	5.3	19.8

* Owl areas and random areas differed significantly at $P \leq 0.0005$.

within 201 ha of plot centers did not differ significantly (range of P, 0.008–0.75), suggesting landscapes around owl areas contained these vegetation types in proportion to availability. Multivariate analysis of the vegetation types within the two sets of ring plots indicated there was no significant difference between owl areas and random areas (MRPP, 1,200 m ring: P = 0.06, 1,600 m ring: P = 0.10).

Landscape pattern indices within 201 ha of plot centers did not differ significantly between owl and random areas (mean patch size: owl = 1.67, random = 1.55, MRPP P = 0.19; mean patch shape index: owl = 1.38, random = 1.36, MRPP P = 0.61; contagion: owl = 39.10, random = 38.69, MRPP P = 0.32). The statistical power of these tests was low (0.24, 0.33, and 0.06 for mean patch size, mean patch shape index, and contagion, respectively). While we acknowledge the limited use of retrospective power analysis (Thomas 1997), we examined the effect sizes necessary to produce significant results. Given our sample size and observed variances (depending on the landscape index considered), the effect sizes would had to have been 2 to 12 times the observed values to increase power to 0.80. Alternatively, power could be increased by increasing the sample size. However, given the observed data and the density of Spotted Owl territories in the area, a study area would have to encompass 1,900–79,000 km^2 to provide significant results.

Description of microhabitat characteristics in young forests.—We located 21 (41%) nest and roost trees in young mixed conifer forest or young forests of ponderosa pine and ponderosa pine-Gambel oak (Fig. 1). Of the eight nests and roosts located in young mixed conifer stands, six had the same or higher percentages of mature mixed conifer forest (median = 20.1%) than young mixed conifer forest (median = 15.0%) within the 201-ha plots. Furthermore, the five owl pairs that nested in young mixed conifer stands chose cavities in mature trees. Hence, we would describe young mixed conifer stands used by owls as young stands with residual large trees. Overall, we located 21 (41%) owl nests and roosts in young and mature mixed conifer forest types.

We found 13 (25%) nest and roost trees in young forests of ponderosa pine and ponderosa pine-Gambel oak (Fig. 1). However, this forest type also contained residual mature or old growth trees not detected during image classification. Of the seven nests located in such forests, all were in cavities of mature Gambel oaks. In addition, five of six (83%) roost stands contained mature trees within a 0.04-ha area around roost trees. Overall, we located 30 (59%) owl nests and roosts in pine or pine-oak forest types.

DISCUSSION

Habitat selection.—Spotted Owls on the study area selected landscapes containing both mature and young mixed conifer forests within 201 ha of nest and roost trees. These mixed conifer forests were characterized by canopy closures ≥55% and, for mature forest, large trees. In areas of young forest, owls used stands with residual large trees in the immediate vicinity of nests and roosts. Mexican Spotted Owl selection of landscapes containing mixed conifer forests and dense canopy cover conditions has been documented previously (see review in Ganey and Dick 1995, Grubb et al. 1997, Peery et al. 1999); however, its relative importance was not demonstrated so clearly as in this study. Mixed conifer forest comprised <5% of our study area, yet 63% of owl areas (201 ha plots) contained such forest.

With the exception of mature open canopy ponderosa pine forest, Mexican Spotted Owls on our study area selected ponderosa pine forests and ponderosa pine-Gambel oak forests in proportion to availability. As with mixed conifer forest, residual large trees in younger forests appeared to be an important microhabitat component for nesting and roosting. Ganey et al. (1999) reported similar results from an area without mixed conifer forest. In addition, they found owls used areas of relatively high canopy closure and suggested that large trees were more important than dense stands of small trees (Ganey et al. 1999).

California and Northern Spotted Owls also nest and roost in young forests that contain residual large trees (Bias and Gutiérrez 1992, Folliard et al. 1993, Moen and Gutiérrez 1997, LaHaye and Gutiérrez 1999). In addition, Thome et al. (1999) found more residual large trees in the territories of Northern Spotted

Owls having high reproductive success than in owl territories having low reproductive success. The use of younger forests with residual large trees may be a case of proximate factors in the environment eliciting a settling response (Hildén 1965). Specifically, the presence of a suitable nest site or variability in alternative roost sites (i.e., to avoid weather or climate fluctuations), both of which residual large trees provide, may be a sufficient cue to elicit settling by Spotted Owls in the Southwest. However, the detection of residual large trees has proven to be difficult in Landsat analysis of Spotted Owl habitat (e.g., Moen and Gutiérrez 1997, this study).

The importance of closed canopy forests to Spotted Owl habitat selection at the landscape scale is unknown. Several hypotheses have been proposed for the selection of closed canopy stands by Spotted Owls at smaller scales; these hypotheses include favorable microclimate conditions (see review in Ganey and Dick 1995), protection from predators (Ganey et al. 1997), and more abundant prey (Gutiérrez 1985, Carey et al. 1992). Ganey and Dick (1995) suggested that evidence favors the microclimate hypothesis for Mexican Spotted Owl selection of nesting and roosting habitat. The data required to evaluate the relative importance of these hypotheses at the landscape scale are limited. However, Svärdson (1949) suggested that a bird may select a territory when the sum of external stimuli reaches a critical threshold level. Therefore, the multiple environmental cues implied in the different hypotheses may combine in different ways to elicit innate settling responses in different Spotted Owls. It also is possible that the occurrence of closed canopy forests at the landscape scale is simply a result of landscape pattern (e.g., clumping of closed canopy forest patches) and coincidental with selection by Spotted Owls at a smaller scale.

Other studies found close associations between Mexican Spotted Owls and old growth mixed conifer and pine forests in the southwestern United States (Ganey and Balda 1994, Zwank et al. 1994, Peery et al. 1999). However, the percentage of old growth and mature forest at owl sites in our study was less than in the above studies. Previous researchers found 42–56% of Mexican Spotted Owl home ranges or territories were in mixed conifer forest, compared to 15% in our study (Ganey and Balda 1994, Zwank et al. 1994, Peery et al. 1999). In addition, we recorded lower amounts of old growth and mature forest within owl areas than reported in the Pacific Northwest (76.3%, Ripple et al. 1991; 58%, Carey et al. 1992; 43.5%, Hunter et al. 1995). Therefore, our results suggested that either Spotted Owls on the study area are not old forest dependent *per se* or they are living in lower quality habitat.

While Spotted Owls on our study area appear to rely less on mature forests of mixed conifer and pine-oak compared to Spotted Owls in other parts of their range, the population on our study area experiences relatively large ($\bar{x}$ = 23%) annual fluctuations (RJG unpubl. data). The amplitude of these fluctuations could be the result of lower quality habitat available for nesting, roosting, and foraging. Further, we do not know the relative fitness potential (*sensu* Franklin et al. 2000) of these young forests. In addition, our highest ecological density (0.212 owls/km^2) was lower than most other Spotted Owl populations. Ecological density was estimated to be 0.48 owls/km^2 for Mexican Spotted Owls (Rinkevich and Gutiérrez 1996), 0.139 owls/km^2 (Bias and Gutiérrez 1992) to 0.40 owls/km^2 (Smith 1995) for California Spotted Owls, and 0.544 owls/km^2 for Northern Spotted Owls (Franklin et al. 1990). All these studies used comparable methods, therefore, direct comparisons are appropriate.

Several studies of the two coastal Spotted Owl subspecies have reported that owl sites have less forest fragmentation than random sites (Lehmkuhl and Raphael 1993, Hunter et al. 1995, Moen and Gutiérrez 1997, Meyer et al. 1998). However, we did not find differences in landscape indices between owl and random areas. This could be due to (1) the scale we chose to conduct the analysis, (2) the difficulty in quantifying landscape pattern (Morrison et al. 1992), (3) the actual absence of a strong difference, or (4) the autocorrelation between the area of vegetation types and landscape parameters (Li and Reynolds 1994). However, at least three other studies found landscape indices of little or no use in predicting Spotted Owl habitat selection (Carey et al. 1992, Ripple et al. 1997, Peery et al. 1999).

Our results support other research that has found the area within 800 m of Spotted Owl nest and roost trees may have the greatest influence on habitat selection (Grubb et al. 1997, Meyer et al. 1998, Swindle et al. 1999). Mean home range size for Spotted Owls near our study area is about 900 ha, or the area within about 1,700-m radius of a nest or roost tree (Ganey and Balda 1989b, Ganey et al. 1999). We did not find evidence of Spotted Owl selection for specific vegetation types beyond 800 m from nest and roost trees. However, Mexican Spotted Owls do use larger areas for foraging (Ganey and Dick 1995, Ganey et al. 1999).

Management implications.—In this breeding season study, Spotted Owls showed the strongest association with closed canopy mixed conifer forests. Although only 4.8% of the study area consisted of mixed conifer forest, 56% of this forest type was contained within 51 201-ha owl areas. Therefore, future management for this species in our study area should strive for the retention of mixed conifer forest for nesting and roosting. In addition, we recommend younger forests be managed for the development or retention of large trees.

The median area of mature closed canopy forest in the 201-ha owl areas was 55 ha; however, this does not indicate a minimum area for protection around owl nests and roosts. Given the amplitude of population fluctuations and relatively low ecological density, protected areas probably should contain more mature forest. Although owls selected most pine and pine-oak forests in proportion to availability, we do not know if the species can persist in these habitats. Additional research will be required to address the relationship between Spotted Owl demographic parameters and habitat quality.

The use of ecological restoration techniques for forest management has received much attention. Such restoration in the southwestern United States involves reductions in basal area of trees, tree density, and canopy cover to return land to presettlement conditions (Covington and Moore 1994, Covington et al. 1997). Ideally, these management practices would produce forests similar to the mature open canopy ponderosa pine forest of this study, the only forest type in which we did not locate any Spotted Owl nest or roost trees. However, it is not clear whether forest structure in areas inhabited by Spotted Owls is similar to forests where ecological restoration has occurred. Ecological restoration experiments have been conducted on relatively flat areas (<15% slope) and on southwestern-facing slopes (Covington and Moore 1994, Covington et al. 1997). In contrast, most Spotted Owl nests and roosts on our study area were located on the lower half of north-facing, moderate ($\bar{x}$ = 27.5%) slopes (RJG unpubl. data). Both slope aspect and percent slope affect fire behavior (Brown and Davis 1973, Whelan 1995); fire exclusion was one primary cause for the postsettlement changes in forest structure (Covington and Moore 1994, Covington et al. 1997). In addition, some historical evidence suggests topographically protected areas such as those inhabited by Spotted Owls may have had the dense structure of older forest (Cooper 1960, Shinneman and Baker 1997).

The importance of mature Gambel oak trees as key nesting sites for owls was evident in our study. Forty percent (34/84) of all nests found during this study were in oak cavities. At least two of these nest trees were felled by firewood cutters during our study even though live oak trees were protected. Oaks are important resources because they may allow not only occupancy of otherwise marginal habitat but also provide food and nest site resources for owl prey. In addition, they are critical resources to game birds (e.g., Wild Turkey, *Meleagris gallopavo*) and avifauna in general (Rosenstock 1998).

Current guidelines for the management of national forests within the range of the Mexican Spotted Owl encompass our recommendations regarding the retention of, and management for, mixed conifer habitat, residual trees, and large oaks (U.S. Dept. of Interior 1995, USDA Forest Service 1996). The primary contribution of this research to existing management plans relates to oaks. First, given the inability of current remote sensing equipment and classification procedures to detect understory oaks, locating this habitat component could be difficult. Therefore, we suggest on site ground verification in stands with dense canopies to estimate oak presence before proposed management activities occur. Second, though standing oaks are protected from harvest, no effective means exists to prevent the poaching of live oaks. Therefore, we continue to recommend protection of all oaks, living or dead, throughout the pine-oak forest within the Mexican Spotted Owl's range (see also Seamans et al. 1999). Piñon-juniper woodlands offer a vast alternative fuel wood resource on our study area, creating no human hardship resulting from oak protection.

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APPENDIX. Definitions of vegetation types and descriptive statistics for map classification of the Mexican Spotted Owl study area, central Arizona, 1994.

Vegetation type	Basal area (m^2/ha) of live trees ≥45.7 cm dbh[a]		Canopy closure (%)	Study area coverage		Classification accuracy (%)	
	All species	Gambel oak		ha	%	Map[b]	Vegetation type[c]
Mature mixed conifer forest	≥6.89		≥55	1,579	2.7	67	80
Young mixed conifer forest	<6.89		≥55	1,228	2.1	91	91
Mature closed canopy forests of ponderosa pine and ponderosa pine-Gambel oak	≥6.89		≥55	7,894	13.5	78	64
Mature open canopy ponderosa pine forest	≥6.89		10–54	8,128	13.9	50	50
Mature open canopy ponderosa pine-Gambel oak forest	≥6.89	≥2.29	10–54	6,842	11.7	67	86
Young forests of ponderosa pine and ponderosa pine-Gambel oak	<6.89	<2.29	<10	22,923	39.2	86	82
Piñon pine-juniper woodland			<10	643	1.1	100	100
Nonforested			<10	9,239	15.8	83	100
Totals				58,476	100.0		

[a] Where values are absent, none were specified.
[b] The number of random locations (n = 88) of a given vegetation type that were classified correctly divided by the total number of random locations that were classified as that vegetation type, multiplied by 100.
[c] The number of random locations (n = 88) of a given vegetation type that were classified correctly divided by the total number of random locations assigned to that vegetation type based on field observation, multiplied by 100.